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OSTEOLOGICAL CHARACTERISTICS
AND AFFINITIES OF THE HEXAGRAMMID
FISHES, WITH A SYNOPSIS¹

By

Jay C. Quast

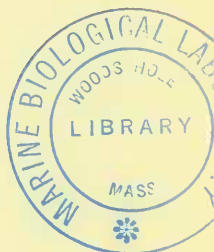
*U.S. Bureau of Commercial Fisheries Biological Laboratory,
Auke Bay, Alaska*

ABSTRACT

Representatives of hexagrammid genera are analyzed for skeletal features, and the findings compared with original and published data on other mail-cheeked fishes (suborder Cottoidei). Perciform groups suggested in the literature as possible mail-cheeked allies are also examined. Results indicate that the fish skeleton has numerous characteristics of taxonomic importance that have been used little or not at all. Examples include caudal structure, dorsal pterygiophore patterns, and ratios between dorsal fin spines, pterygiophores, and vertebrae. Taxonomic findings indicate that the present classification of mail-cheeked fishes, based on Regan's work of 1913, is in need of revision. The Hexagrammidae and Zaniolepididae are probably primitive offshoots of the cottid evolutionary line and the three groups should be placed in the same superfamily. The zaniolepidids are generally intermediate between the hexagrammids and cottids. The Anoplo-

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pomatidae (*Anoplopoma*, *Erilepis*) are sufficiently distinct from the scorpaenids and hexagrammid-cottids to warrant a separate superfamily. The mail-cheeked fishes may be an artificial assemblage containing at least three distinct evolutionary lines, scorpaenid, anoplopomatid, and hexagrammid-cottid. The findings are summarized in a synopsis.

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INTRODUCTION

The nine extant species of the family Hexagrammidae form an important element in the mail-cheeked fish fauna of the North Pacific Ocean. The phyletic position of the family within the mail-cheeked fishes (suborder Cottoidei) has been uncertain with considerable difference of opinion concerning where the family lines should be drawn. To investigate these and related questions, I undertook an osteological study of the family and its purported members and allies as part of my doctoral problem at the University of California at Los Angeles.

The mail-cheeked families listed by Berg (1940) and the Serranidae and Cirrhitidae are compared for features of cranium, axial skeleton, and appendicular skeleton. The Serranidae and Cirrhitidae are included because one or both of these families are usually mentioned by students of the phylogeny of the mail-cheeked fishes, e.g. Gill (1889), Jordan and Evermann (1898), and Regan (1913). The findings, as brought out in the discussion, indicate that considerable changes should be made in the arrangement of the families in the suborder and that the suborder is probably polyphyletic. To facilitate comparisons, the findings are summarized in a synopsis, with special emphasis on comparisons with the Hexagrammidae.

Taxonomic changes in several species follow the recommendations of Quast (1960): *Orylebius pictus* and *Ophiodon elongatus* are in monotypic subfamilies under the Hexagrammidae; the Japanese *Agrammus agrammus* is placed in the genus *Heragrammos*; and the nominal species *Heragrammos superciliosus* and *H. lagocephalus* are synonymized under *H. lagocephalus*.

MATERIALS AND METHODS

Skeletal material included X-ray photographs, boiled fresh specimens, Chlorox- or Purex-treated preserved material, and dissections (table 1). Dissection and study of skeletal material were sometimes facilitated by alizarin staining, with the specimens being dissected to the vicinity of the skeletal elements to aid stain penetration. Techniques of Green (1952) generally were followed except for storage of specimens in a 50 per cent isopropyl alcohol solution before fine dissections. Clearing in glycerine, was avoided when further examination was contemplated because of resultant slipperiness and irregularities of light refraction.

In skeletal preparations the entire fish was immersed in very hot, but not boiling, water with a detergent. Skeletal elements were removed as they loosened and were cleaned with a toothbrush. Care was taken not to cook the fish so extensively that neurocranial bones became separated or vertebral column and hypural fan became disarticulated. Jets of water and air were useful for removing soft tissues after cooking. When dry, some fatty bones were degreased by soaking for a week or more in toluene or xylene.

No one method of preparation is entirely satisfactory for material used in osteological studies, and two or more methods should be used on separate specimens of the same species when possible. Although dry skeletal preparations are superior for neurocranial study, dissections and alizarin stain-

TABLE 1.

Number of specimens examined

Symbols for the columns represent method of examination: X, X-ray; S, alizarin staining; C, cooked or Clorox-treated material.

	X	S	C
Holocentridae			
<i>Holocentris suborbitalis</i>	1		
<i>Myripristis clarionensis</i>	1		
Serranidae			
<i>Alphestes galapagensis</i>	1		
<i>Alphestes multiguttatus</i>	2		
<i>Dermatolepis punctata</i>			1
<i>Diplectrum macropoma</i>	1		
<i>Epinephelus analogus</i>			1
<i>Mycteroperca jordani</i>			1
<i>Paralabrax auroguttatus</i>	1		
<i>Paralabrax clathratus</i>		1	
<i>Paralabrax nebulifer</i>	1		
<i>Paranthias colonus</i>	1		1
<i>Stereolepis gigas</i>			1
Centrarchidae			
<i>Micropterus salmoides</i>	1		
Sciaenidae			
<i>Micropogon altipinnis</i>	1		
Cichlidae			
<i>Cichlasoma dori</i>	1		
Pomacentridae			
<i>Eupomacentrus beebei</i>	1		
Cirrhitidae			
<i>Cirrhitus marmoratus</i>	1		
<i>Cirrhitus rivulatus</i>		1	1
<i>Paracirrhites arcatus</i>	1		
Scorpaenidae			
<i>Dendrochirus chloreus</i>		1	
<i>Pterois antennata</i>	1		
<i>Scorpaena guttata</i>	1		1
<i>Scorpaena mystes</i>	1		
<i>Scorpaena</i> sp.....			1
<i>Sebastiscus marmoratus</i>	1		
<i>Sebastodes chlorostictus</i>	1		1
<i>Sebastodes melanops</i>		1	
<i>Sebastodes paucispinis</i>	1		

TABLE 1.—Continued

Scorpaenidae—Cont.	X	S	C
<i>Sebastodes serripes</i>			1
<i>Sebastolobus alascanus</i>	1		
<i>Sebastolobus altivelis</i>	2	1	
Triglidae			
<i>Prionotus albiostris</i>	1		
<i>Prionotus stephanophrys</i>	1		1
Hexagrammidae			
<i>Hexagrammos agrammus</i>	16		1
<i>Hexagrammos decagrammus</i>	20		3
<i>Hexagrammos lagocephalus</i> ¹	38	1	1
<i>Hexagrammos octogrammus</i>	20		
<i>Hexagrammos otakii</i>	12		
<i>Hexagrammos stelleri</i>	24		
<i>Ophiodon elongatus</i>	19	1	2
<i>Oxylebius pictus</i>	39	1	1
<i>Pleurogrammus monopterygius</i>	10		
Zaniolepididae			
<i>Zaniolepis frenata</i>	4		
<i>Zaniolepis latipinnis</i>	6	1	1
Anoplopomatidae			
<i>Anoplopoma fimbria</i>	2	1	3
<i>Erilepis zonifer</i>	3		
Platycephalidae			
<i>Platycephalus</i> sp.....		1	
Cottidae			
<i>Artemius notospilotus</i>	2		1
<i>Chitonotus pugetensis</i>			1
<i>Clinocottus analis</i>			3
<i>Cottus bairdii</i>			1
<i>Enophrys bison</i>			1
<i>Hemilepidotus hemilepidotus</i>	1		1
<i>Icelinus</i> sp.....			4
<i>Leptocottus armatus</i>			2
<i>Leiocottus hirundo</i>	1		
<i>Oligocottus</i> sp.....			2
<i>Radulinus</i> sp.....			1
<i>Scorpaenichthys marmoratus</i>	1	1	2
Cyclopteridae			
<i>Liparis dennyi</i>	2		
<i>Liparis florum</i>	2		

¹ Includes *H. superciliosus*.

ing, or clearing and staining, are more useful for other skeletal parts. Conventional X-rays are of little value for head structure or fine osteological detail.

Skeletal terminology follows Harrington (1955) for the neurocranium, and Starks (1901) and Merriman (1940) for vertebrae, ribs, and caudal

skeleton. The term "pterygiophore," standardized by Eaton (1945), is employed for the median fin supports. Names and arrangements of taxonomic groups follow Berg (1940) except for erection of the family Zaniolepididae. (For reference figures of generalized serranid and scorpaenid skeletons see Starks (1898, 1901).)

OSTEOLOGY

Splanchnocrania of the families Serranidae, Cirrhitidae, Scorpaenidae, Hexagrammidae, Zaniolepididae, and Cottidae are closely similar and appear to have only a few trenchant differences at the family level. Size and arrangement of toothed upper pharyngeals and number of branchiostegals may differentiate some families. There are considerable differences in shape and degree of development of splanchnocranial elements between species and genera within some families (for example, see Matsubara, 1943), and family lines are very difficult to draw for these structures. None of the families show the extreme flattening of the skull exhibited by *Platycephalus*. Preopercular spines are absent in all hexagrammids except *Ophiodon*, which has them feebly developed.

TOOTHED UPPER PHARYNGEALS.

The number of paired upper pharyngeal bones is important to the taxonomy of the mail-checked fishes. This was first recognized by Cope (1871), who stresses this character in addition to the presence or absence of a myodome. Gill (1889) discusses Cope's taxonomic use of the upper pharyngeals and concludes that they are probably not of great importance. However, Regan (1913) finds them useful and includes them in his synoptic key and discussion.

The representatives of the Serranidae, Cirrhitidae, Scorpaenidae, Hexagrammidae, Zaniolepididae, and Anoplopomatidae have three separate pairs of toothed upper pharyngeals. Similar number and arrangement are figured for *Roccus saxatilis* by Merriman (1940), for *Sebastolobus alascanus* by Starks (1898), and for Platycephalidae by Matsubara and Ochiai (1955). All species with three pairs have the upper pharyngeals attached to branchial arches 2-4. Cottid representatives (three genera, three species examined) contrast in having only two pairs of upper pharyngeals (or but one pair in some representatives according to Taranets, 1941). The paired pharyngeals of the cottids occupy arches 2-4 and the third and fourth arches lead to the second pharyngeal only instead of the second and third pharyngeals as in the other families. The evidence strongly supports Regan's view that the large second upper pharyngeal of Cottidae actually represents coalescing of primitively separate second and third elements.

Although hexagrammids and zaniolepidids resemble the serranids, cirrhitids, scorpaenids, anoplopomatids, and platycephalids in having three

pairs of upper pharyngeals, they differ by having the last pair reduced in size. In all but *Orylebius pictus*, the third pair is less than one-half the size of the first pair. In *O. pictus* the size is larger, slightly greater than one-half. In *Anoplopoma fimbria* the first and third pairs are of approximately the same size and only slightly smaller than the second; in *Erilepis zonifer* the first pair is considerably smaller than the second.

Upper and lower pharyngeals have simple teeth of approximately the same size as those in the jaws in all hexagrammid genera but *Ophiodon*, which has canine jaw teeth. All Serranidae, Cirrhitidae, and mail-cheeked fishes have one pair of lower pharyngeals.

BRANCHIOSTEGALS.

Six branchiostegals are found in the Hexagrammidae, Zaniolepididae, Anoplopomatidae, and most Cottidae. The uppermost and outermost is attached to the epihyal and the next branchiostegal is attached to or slightly lateral to the epihyal-ceratohyal junction. Two more are attached to the lateral, wide section of the ceratohyal, and the innermost two are on the medial, narrow part. The branchiostegal arrangement of the group is the same as that of *Cirrhitus rivulatus*, which differs, however, in having the innermost ray shortened considerably. According to Jordan and Evermann (1905), cirrhitid branchiostegals number from three to six, and usually six.

Seven branchiostegals characterize the Serranidae, Scorpaenidae, Triglidae, and Platycephalidae examined by boiling or staining. The additional branchiostegal not found in the hexagrammids and cottids appears to be one of three attached to the innermost, narrow portion of the ceratohyal. Jordan and Evermann (1905) characterize the serranids as having "normally 7 (occasionally 6)" branchiostegals and Matsubara (1943) found a similar branchiostegal number and arrangement for all but three of 33 scorpaenoid genera; *Cocotropus*, *Aploactis*, and *Erispher* have six rays.

NEUROCRANIUM

SUBORBITAL BONES

The well-developed suborbital stay of the hexagrammids conforms most closely to the scorpaenid type 2 described by Matsubara (1943). Its posterior extremity is truncate and attached to the preopercle. However, the attachment does not appear to be as firm as that in the scorpaenoid fishes.

Five was the maximum number of suborbital elements, excluding the lachrymal, found in the pereiform groups. Among the mail-cheeked fishes, the hexagrammids and some marine cottids show the most generalized condition in which the postorbital suborbitals lie separately between the second suborbital and the sphenotic. The fifth, uppermost suborbital of the hexagrammids lies over the sphenotic projection, bearing the same relationship

to the sphenotic as in other representatives of the mail-cheeked fishes. It is undoubtedly the same as Allis' (1909) prefrontal and Harrington's (1955) dermosphenotic. *Zaniolepis* has only one free suborbital behind the orbit: the dermosphenotic is firmly attached to the sphenotic and the second and third suborbital elements appear to be fused. In his figures of freshwater cottids and comephorids of Lake Baikal, Taliev (1955) shows from one to all of the last three suborbitals missing. *Anoplopoma* also has a reduced condition in which only one of the last three is evident. In *Cirrhitus* and the serranids and scorpaenids, the fifth suborbital (dermosphenotic) is firmly attached to the sphenotic. Matsubara (1943) found a high degree of variation in the scorpaenids and their allies in regard to presence or absence of the third and fourth suborbitals.

SUPRATEMPORAL CANAL

This sensory canal extends dorsally from the junction of pterotic and main lateral line canals to the skull vertex. In the Serranidae and Cirrhitidae each supratemporal canal transverses three small scale bones that are free from the skull, a relationship very similar to that shown for *Perca* by Cuvier and Valenciennes (1828). In the mail-cheeked fishes, the ossicles carrying this canal appear to be fused to the parietals, and are actually fully enclosed by a posterior parietal ridge in some forms. These findings agree with those of Allis (1909), who discusses and figures these elements for representatives of varied fish groups, including several mail-cheeked forms. They agree also with Harrington (1955), who discusses the canal's homologies in various teleost groups.

Important differences in the arrangement of this canal distinguish some hexagrammids, cottids, and some other mail-cheeked fishes. Frequently the differences are visible in figures from the literature. In the hexagrammids, zaniolepidids, and some cottids, the supratemporal canal is in the form of a raised bony tube on the dorsal surface of the parietal (figure 1). It traverses the middle or anterior sections of the parietal in all hexagrammids except *Ophiodon*, in which it extends along the posterior parietal margin. In the scorpaenids, *Anoplopoma*, and other cottids, in contrast, the supratemporal canal is enclosed by the posterior margin of the parietal and emerges near the midline, never appearing in the form of a raised bony tube.

The first accessory lateral line in the two species of *Hexagrammos* that were examined for this feature (*H. decagrammus* and *H. lagocephalus*) was found to originate on the occiput at the junction of the supratemporal canals, with the lumen of the line and the canals seeming to be continuous. Rutenberg (1955) figures and describes the supratemporal canals in representatives of two hexagrammid genera and uses their weak development in *Pleurogrammus* (figure 1) as an argument for separating this genus as a distinct subfamily.

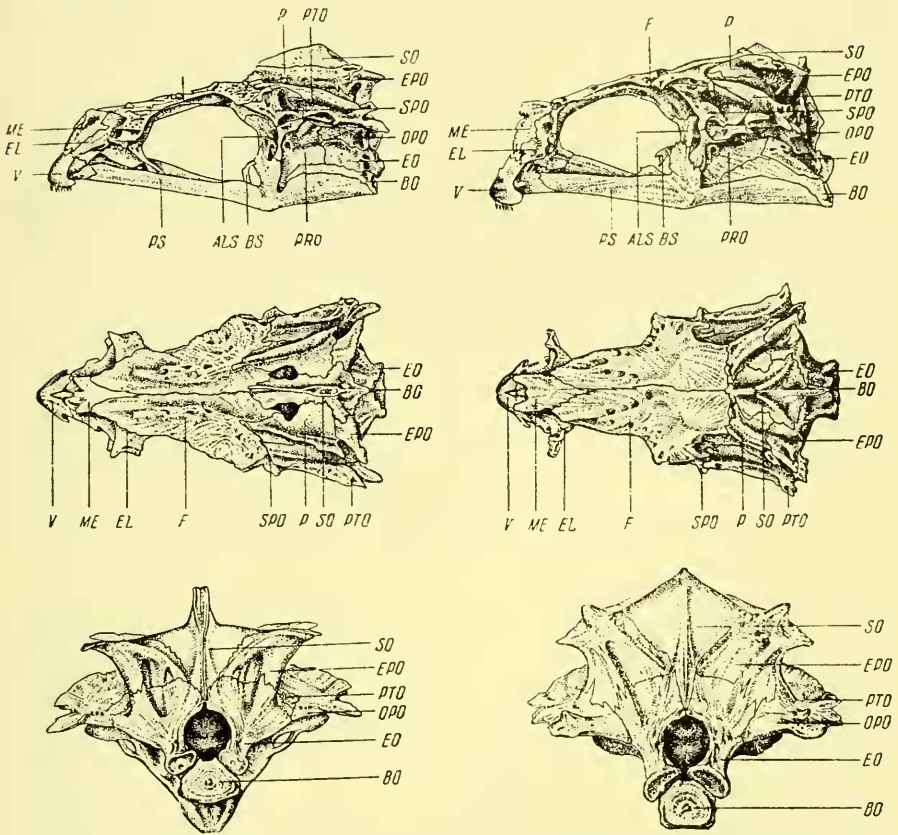


FIGURE 1. Neurocrania of *Pleurogrammus monopterygius* (left) and *Hexagrammos lagocephalus* (right). Note the large foramina in the cranial roof of *P. monopterygius*, as well as the widely separated anterior openings of the supra-temporal canals in this species. ALS — pterosphenoid; BO — basioccipital; BS — basisphenoid; EL — lateral ethmoid; EO — exoccipital; EPO — epiotic; F — frontal; ME — mesethmoid; OPO — opisthotic; P — parietal; PRO — prootic; PS — parasphenoid; PTO — pterotic; SG — supraoccipital; SPO — sphenotic; V — vomer. (From Rutenberg, 1955.)

OPISTHOTICS.

The size and forward contacts of the opisthotics vary considerably among representatives of the mail-checked fishes, as shown by Regan (1913). The specimens at hand were surveyed in this regard: in all serranids, the large opisthotic extends forward to a sutural contact with the prootic, a relationship true also for *Cirrhitus*, the scorpaenids, *Prionotus*, all hexagrammids (except *Ophiodon*), *Zaniolepis*, and *Platycephalus*. In *Ophiodon*, *Anoplopoma*, and the Cottidae examined, an area of the pterotic intervenes

between the prootic and a small opisthotic. Taliev (1955) shows a small opisthotic in his figures of the Lake Baikal cottids and comephorids.

EXOCCIPITALS.

In the serranid representatives (and five species of *Roccus* figured by Woolcott, 1957) the exoccipitals are in contact below the foramen magnum, as also in *Cirrhitis* and species of *Sebastodes*. In *Scorpaena*, hexagrammids, zaniolepidids, *Anoplopoma*, and cottids, the exoccipitals are not visibly in contact in the region of the foramen magnum. The hexagrammid genus *Oxylebius* shows an intermediate condition in which the exoccipitals are well separated on the floor of the foramen magnum but contact anteriorly.

PARASPHENOID-PTEROSPHENOID JUNCTION.

The Hexagrammidae, Zaniolepididae, Cottidae, *Anoplopoma*, Agonidae, and Cyclopteridae are distinguished from the Scorpaenidae and other mail-cheeked fishes by a junction of the ascending lateral wing of the parasphenoid with the pterosphenoid element on each side of the neurocranium (figure 2). This character was first utilized for the systematics of the mail-cheeked fishes by Gill (1889). In the more generalized condition found in serranids (usually) and scorpaenids, the prootic clearly separates the parasphenoid and pterosphenoid at the orbital surface; this simple relationship is figured for various species of *Sebastodes* by Cramer (1895), and Matsubara (1943) indicates in his figures that the simple arrangement holds for scorpaenid fishes in general. The presumed derived condition where parasphenoid and pterosphenoid are conjoined also occurs in the cottids and comephorids of Lake Baikal, according to the figures of Taliev (1955), and Rendahl (1934) figures this condition for *Hypsagonus quadricornis*.

The serranids do not uniformly show the simple condition. *Dermatolepis punctata* is unique among the serranids investigated in having the parasphenoid and pterosphenoid conjoined, much as the Hexagrammidae and Cottidae (in other respects the neurocrania are dissimilar). The opposite case occurs in the reputed anoplopomatid *Erilepis zonifer*, whose family status should be reviewed. In *E. zonifer* the parasphenoid and pterosphenoid are widely separated, whereas in *Anoplopoma* not only are the two elements in contact but the parasphenoid also conjoins with the frontal element.

One possible mode of origin of the junction is suggested by the arrangement found in *Cirrhitis* and *Scorpaena*, in which the parasphenoid and pterosphenoid are narrowly separated by a notch. But an even more provocative situation was found in the arrangement of ligaments and bones in *Sebastodes* spp. and *Erilepis zonifer*. In these examples the parasphenoid and pterosphenoid do not contact but the space between the two is bridged by a ligament, which if ossified toward its center from the two bones would effect their junction. The parasphenoid-pterosphenoid junction appears

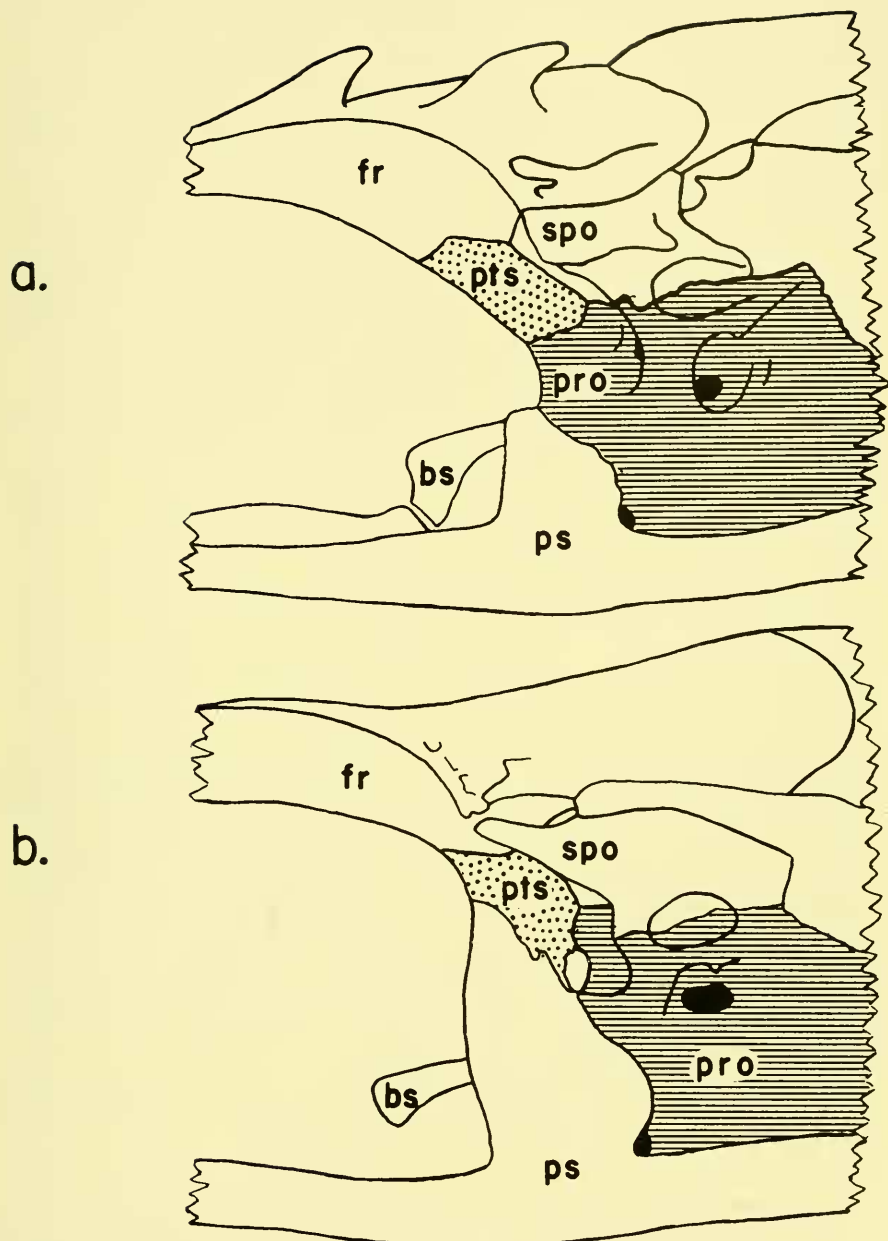


FIGURE 2. Posterior orbital region of the neurocrania of two spiny-rayed fishes. Two relationships between the posterior orbital elements are illustrated: *a*, the parasphenoid and pterosphenoid separated by a broad gap and the prootic bordering the orbit (*Sebastodes sericeus*); *b*, the parasphenoid and pterosphenoid in contact, forming a new foramen anterior to the prootic (*Oxylebius pictus*). *bs* — basisphenoid; *fr* — frontal; *pro* — prootic; *ps* — parasphenoid; *pts* — pterosphenoid; *spo* — sphenotic.

to be consistent in the hexagrammid-cottid evolutionary line despite the exceptions found in the other groups; it is a reliable taxonomic character for separation of the scorpaenoid fishes from the hexagrammids, zaniolepidids, and cottids.

BASISPHENOID.

Presence or absence of the basisphenoid is a character of importance in Regan's system and was found to be generally consistent in the families I examined. This median bone originates at or above the parasphenoid in the membranous interorbital septum and bends upward and posteriorly to its T-shaped termination, which contacts inwardly directed processes of the prootics. The inwardly directed prootic processes may also meet behind the basisphenoid to form a "prootic bridge" (Rendahl, 1934b). The bridge thus formed separates the optic nerves and the anterior section of the brain above from the myodome (the canal containing the rectus eye muscles) below. Posterior to the prootic bridge, the pituitary fossa connects the brain cavity with the myodome cavity. The prootic wings meet again behind the pituitary fossa to complete the floor of the cranial cavity and the roof of the myodome.

According to Regan, the presence of a basisphenoid distinguishes the Scorpaenidae and Hexagrammidae from the cottids, comephorids, and agonids. My investigations and the works of Taliev and Rendahl generally support this view. Two minor exceptions have been noted in the literature. Matsubara (1943) found the genus *Setarches* to be exceptional among the scorpaenoid fishes in the lack of a basisphenoid, and Gutberlet (1915), without comment, figures the skull of the primitive cottid *Scorpaenichthys marmoratus* with a basisphenoid. The prootic supports for the basisphenoid are surprisingly well developed in this species and it seems possible that Gutberlet had an aberrant specimen. However, this element was lacking in all specimens I examined and I am inclined to believe that he was in error.

The loss of the basisphenoid in the cottids and agonids seems associated with the general reduction of the cranial floor in these fishes. In the families with a well developed basisphenoid, e.g. Serranidae, Scorpaenidae, and Hexagrammidae, the cranial floor is usually normal.

LATERAL ETHMOIDS.

Considerable variation occurs both between and within the mail-checked fish families in regard to the development of the lateral ethmoids and in regard to number and position of the facets for articulation with the lachrymal and palatine bones. These characters are unsatisfactory for the differentiation of either the Hexagrammidae or the Cottidae, although they may be of value in the systematics of lower ranks within the families.

VERTEBRAE AND ASSOCIATED STRUCTURES

VERTEBRAE (INCLUDING UROSTYLE)²

In his diagnosis of the Hexagrammidae, Regan gives the vertebral number range as 42–64. Although he includes *Oxylebius* in the family, he fails to include its vertebral count in the family diagnosis. With the inclusion of the *Oxylebius* range, with a minimum of 37, the family Hexagrammidae and the Scorpaeniformes of Regan (Scorpaenoidae of Berg, 1940) are no longer completely distinct.

The families investigated appear to overlap widely in vertebral morphology and no consistent family differences can be drawn. In *Hexagrammos* and *Ophiodon* the parapophyses are more strongly developed and project more laterally than in the serranids and scorpaenids, but *Oxylebius* resembles the serranids and scorpaenids more closely in this respect. The contrasting development of the parapophyses that Gill (1889) implies as a differentiating character between the cottids and hexagrammids is not consistent within the families; the cottid *Scorpaenichthys marmoratus* is very similar to *Hexagrammos*. Width and length measurements on caudal vertebrae (the fourth before the urostyle was chosen as representative) disclose a general tendency in the hexagrammids for the vertebrae to be shorter in respect to their width as species vertebral number increases, as might be expected. However, the ratio is not of taxonomic value because hexagrammid ranges broadly overlap those of other families. A tendency toward reduction of the first neural spine noted for cottids is not apparent in the serranids, cirrhitids, scorpaenids, hexagrammids, zaniolepidids, or anoplopomatids.

The proportion of precaudal vertebrae in the hexagrammids ranges between 34–46 per cent. This is beyond both the upper and lower limits of the serranid, cirrhitid, and scorpaenid representatives, which have an inclusive range of 36–42. Hexagrammid values broadly overlap those of the cottids (39–42 per cent) and exceed those of *Eritepis* and *Anoplopoma* (22–31 per cent). The zaniolepidids (33 per cent) are slightly below the lower limit of the Hexagrammidae, within the range of the Cottidae, and above the upper limit of the Anoplopomatidae.

Percentage of precaudal vertebrae with parapophyses bridged by a haemal arch varies considerably among the families. The highest, 50 per cent, characterizes *Cirrhitus rivulatus*. *Hexagrammos* (*H. decagrammus* and *H. lagocephalus*) and *Oxylebius* vary from 35–43. In *Ophiodon* the proportion is the lowest, usually with only one precaudal vertebra, or 4 per cent of an average of 23, bridged.

Autogenous haemal arches in the hexagrammids are normally limited to the last two caudal vertebrae before the urostyle (table 2).

² "Urostyle" is here used as synonymous with the longer but more descriptive term "urostyler half-vertebra" of Gosline (1961).

TABLE 2.

Occurrence of terminal caudal vertebrae with autogenous haemal arches, Hexagrammidae.

Species	Number of vertebrae	Per Cent having 2	Number of specimens
<i>Hexagrammos agrammus</i>	2-3	81	16
<i>H. aecagrammus</i>	2-3	83	59
<i>H. lagocephalus</i> ¹	2-3	89	44
<i>H. octogrammus</i>	2-3	91	35
<i>H. otakii</i>	2-3	82	11
<i>Ophiodon elongatus</i>	2-3	96	27
<i>Oxylebius pictus</i>	2-3	93	30
<i>Pleurogrammus monoptyrygius</i>	2-4	71	7

¹ Includes *H. superciliosus*. Thirty-nine specimens are from the eastern Pacific and Aleutian Islands and 5 are from the western Pacific.

RIBS.

In his synopsis of the families and superfamilies of mail-cheeked fishes, Gill (1889) states that the Scorpaenoidae (including the Hexagrammidae) have "ribs, typically, borne on enlarged parapophyses," distinguishing them from the Cottoidae, which have "ribs sessile on the vertebrae." However, in making this distinction between the two groups, he does not note that the mail-cheeked fishes have two types of ribs, pleural and epipleural, and also that the pleural ribs are absent from more precaudal vertebrae in the cottids than in the scorpaenids and hexagrammids. Regan (1913) establishes this second difference between the two groups and his findings are verified by my examinations. The hexagrammids, *Zaniolepis*, and *Anoplopoma* differ from the serranids and scorpaenids in having the epipleural and pleural ribs inserted together on the vertebral parapophyses. In the serranids and scorpaenids, epipleural ribs are inserted on the pleural ribs themselves for at least the first four pleural ribs — a relationship figured for *Roccus saratilis* by Merriman (1940) and *Sebastolobus alascanus* by Starks (1898). According to Regan, all ribs are absent in the scorpaeniform families Caracanthidae, Aploactidae, and Synancejidae; the unusual situation he describes for the Platyccephaliformes, the pleural ribs attached to the epipleurals, was verified by examination of one representative. In all the percoid representatives I list, the series of epipleural ribs begins on the first vertebra with at least the first two sessile on their vertebrae. Pleural ribs, when present, begin on the third to fifth vertebra in all groups except the cottids.

DORSAL PTERYGIOPHORES.

Despite abundant published osteological studies of teleosts and figures of

the axial skeleton that show important differences in arrangement of the dorsal pterygiophores, there has been little attempt to classify the various arrangements and use the patterns for taxonomic purposes. Matsubara (1943) discusses various arrangements in the scorpaenoid fishes but makes no comparisons with other mail-cheeked groups, or with the acanthopterygian fishes in general. Dramatic and apparently consistent differences that are probably of taxonomic importance exist between various fish groups.

Pterygiophores are doubled in one or more of the anterior interneural spaces beneath the spinous dorsal fin in a large number of acanthopterygian fishes. Representative arrangements of these bones in single species are illustrated in figures of *Roccus saxatilis* (Starks, 1901; Merriman, 1940), *Archoplites interruptus* (Dineen and Stokely, 1956), and *Sebastes viviparus* (Andriashev, 1954). In addition, I found the condition to be consistent in representatives of the following families: Holocentridae (2 genera, 2 species), Serranidae (4 genera, 6 species), Centrarchidae (1 species), Sciaenidae (1 species), Cichlidae (1 species), Pomacentridae (1 species), Cirrhitidae (2 genera, 3 species), Scorpaenidae (5 genera, 8 species), Triglidae (2 genera, 2 species), Anoplopomatidae (2 genera, 2 species), and Platycephalidae (1 species).

Representatives of the Hexagrammidae (except *Ophiodon*), Zaniolepididae, Cottidae, and Cyclopteridae normally differ from the scorpaenoid fishes (except *Parabrachirus*) in having a single pterygiophore in each interneural space beneath the dorsal fin (*Oryzias pictus* rarely has a doubled pterygiophore in the second space).

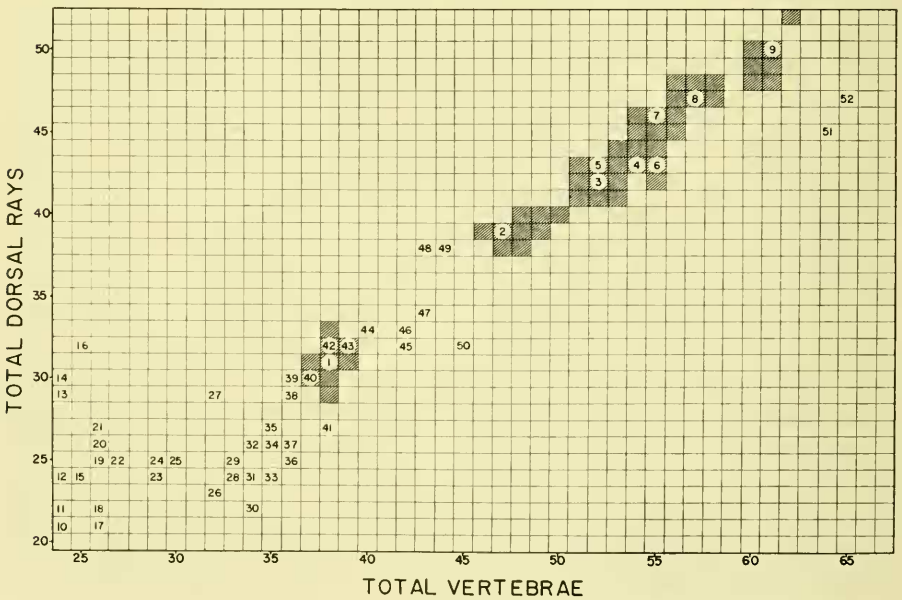
Ophiodon elongatus is exceptional among the hexagrammid fishes, and acanthopterygian representatives for which X-rays or published illustrations are available, in having a combination of doubled dorsal fin spines and a first dorsal pterygiophore of doubled structure at the first interneural space (between the cranium and the first neural spine). Oddly, this arrangement is not a serious violation of the one-to-one arrangement between pterygiophores and vertebrae beneath the spinous dorsal fin that characterizes the hexagrammid fishes, because a compensating gap in the pterygiophore series occurs more posteriorly in *Ophiodon*, discussed below. Because of this compensating arrangement, I regard *O. elongatus* as basically consistent with the general hexagrammid one-to-one pattern. The occurrence of this pattern in the zaniolepidids and cottids is additional evidence for the close affinity between the three families. The one-to-one arrangement is also found in some other, presumably unrelated, percoid groups and is figured for *Perca* by Cuvier and Valenciennes (1828) and for representatives of four families of northern eel-like blennioids by Andriashev (1954). Some degree of doubling of dorsal pterygiophores in their spaces probably characterizes the overwhelming majority of other perciform fishes.

DORSAL RAY TOTALS.

The hexagrammids show a close interspecific correlation between sums for dorsal rays and vertebrae. The dorsal rays and their associated pterygiophores normally occupy approximately 81 per cent of the interneural spaces above the vertebral column. When plotted graphically, proportions for the various hexagrammid species form a nearly straight regression line that differentiates them from the proportions obtained for numerous other percid-form representatives (figure 3). Significantly, the Zaniolepididae and Cottidae, which have close affinities with the Hexagrammidae on the basis of other osteological evidence, also show similar proportions (figure 3).

Several anatomical factors are responsible for the distinct relationships between dorsal rays and vertebrae that characterize some fish groups (figure 3). The hexagrammid proportions reflect a high vertebral number, a one-to-one relationship between the pterygiophores (with their associated dorsal fin rays) and the interneural spaces, and a constant extent (percentage-wise) of the vertebral column that is occupied by the dorsal fin and its supporting elements.

When first examined, specimens of *Ophiodon elongatus* appeared to be an exception among the hexagrammid fishes because the dorsal spines are doubled over the first interneural space. This arrangement would give a sum for dorsal spines one in excess of that for associated neural spines and vertebrae if the usual hexagrammid arrangement, one element per inter-



neural space, were followed. However, in the 20 *Ophiodon* specimens examined, the total number of dorsal fin spines was equal to the total number of neural spines. In each specimen the dorsal pterygiophore and its dorsal fin spine was absent in an interneural space somewhere between vertebrae 12 and 16. Investigation shows that *Ophiodon elongatus* is not unique in this arrangement—*Erilepis zonifer* and the holocentrid representatives were found to lack a pterygiophore and its spine. The absence of a pterygiophore and spine may also be observed in figures of *Perca* by Cuvier and Valen-

FIGURE 3. Ratios between sums for dorsal fin rays and vertebrae in hexagrammids and representatives of other spiny-rayed fishes. Numerals represent modal frequencies for ratios of hexagrammid species or individual ratios for non-hexagrammids. Hatched region gives the hexagrammid range of variation. Species key below:

- | | |
|---|--|
| 1. <i>Oxylebius pictus</i> | 26. <i>Micropterus salmoides</i> |
| 2. <i>Hexagrammos agrammus</i> | 27. <i>Cichlasoma doriai</i> |
| 3. <i>Hexagrammos otakii</i> | 28. <i>Artedius notospilotus</i> (in part) |
| 4. <i>Hexagrammos stelleri</i> | <i>Clinocottus analis</i> (in part) |
| 5. <i>Hexagrammos octogrammus</i> | 29. <i>Clinocottus analis</i> (in part) |
| 6. <i>Hexagrammos lagocephalus</i> | 30. <i>Icelinus</i> sp. (in part) |
| 7. <i>Hexagrammos decagrammus</i> | 31. <i>Artedius notospilotus</i> (in part) |
| 8. <i>Ophiodon elongatus</i> | 32. <i>Oligocottus</i> sp. (in part) |
| 9. <i>Pleurogrammus monopterygius</i> | 33. <i>Icelinus</i> sp. (in part) |
| 10. <i>Scorpaena guttata</i> , <i>S. mystes</i> | 34. <i>Leiocottus hirundo</i> , |
| 11. <i>Pterois antennata</i> , | <i>Icelinus</i> sp. (in part) |
| <i>Diplectrum macropoma</i> | 35. <i>Oligocottus</i> sp. (in part) |
| 12. <i>Paralabrax auroguttatus</i> , | 36. <i>Leptocottus armatus</i> |
| <i>P. nebulifer</i> | 37. <i>Chitonotus</i> sp. |
| 13. <i>Alphestes galapagensis</i> , | 38. <i>Scorpaenichthys marmoratus</i> |
| <i>A. multiguttatus</i> (in part) | 39. <i>Hemilepidotus hemilepidotus</i> |
| <i>Paranthias colonus</i> | (in part) |
| 14. <i>Alphestes multiguttatus</i> (in part) | 40. <i>Hemilepidotus hemilepidotus</i> |
| 15. <i>Sebastiscus marmoratus</i> | (in part) |
| 16. <i>Micropogon altipinnis</i> | 41. <i>Icelinus</i> sp. (in part) |
| 17. <i>Cirrhitus marmoratus</i> , | 42. <i>Radulinus</i> sp. |
| <i>Paracirrhitus arcatus</i> , | 43. <i>Liparis florae</i> (in part) |
| <i>Prionotus stephanophrys</i> | 44. <i>Liparis florae</i> (in part) |
| 18. <i>Prionotus albiostris</i> | 45. <i>Zaniolepis latipinnis</i> |
| 19. <i>Myripristis clarionensis</i> | 46. <i>Zaniolepis frenata</i> (in part) |
| 20. <i>Sebastodes chlorostictus</i> | 47. <i>Zaniolepis frenata</i> (in part) |
| 21. <i>Eupomacentrus beebei</i> , | 48. <i>Liparis dennyi</i> (in part) |
| <i>Sebastodes paucispinis</i> | 49. <i>Liparis dennyi</i> (in part) |
| 22. <i>Holocentrus suborbitalis</i> | 50. <i>Erilepis zonifer</i> |
| 23. <i>Sebastolobus altivelis</i> (in part) | 51. <i>Anoplopoma fimbria</i> (in part) |
| 24. <i>Sebastolobus altivelis</i> (in part) | 52. <i>Anoplopoma fimbria</i> (in part) |
| 25. <i>Sebastolobus alascanus</i> | |

ciennes (1828) and in a figure of the freshwater centrarehid *Archoplites interruptus* by Dineen and Stokely (1956).

Representatives of the cottid genera *Hemilepidotus* and *Scorpaenichthys* closely approximate the hexagrammid fishes in pterygiophore arrangement as well as in the ratio between pterygiophores and vertebrae. It is interesting, and of possible evolutionary significance, that *Erilepis*, *Anoplopoma*, and *Zaniolepis* would fall within or closely approximate the hexagrammid region of figure 3 if the rays and/or pterygiophores that are lacking in the anteriormost interneural spaces of these genera were present, as they are in the Hexagrammidae.

CAUDAL SKELETON.

The apparent basic plan for hypural arrangement in the perciform caudal skeleton is that of three upper and lower hypurals that either articulate with or are fused to the urostyle, or "urostyler half-vertebra," to use the terminology of Gosline (1961). Hypural numbering has been standardized by Gosline to designate the lowest (anteriormost) as the first and the uppermost as the sixth. Also, the first hypural seems always to bear a spinelike lateral process on each side that is associated with a foramen posteriorly. The upper and lower sets of primitively free hypurals can nearly always be readily distinguished by a fairly wide gap that separates them near the midline. The generalized hypural arrangement is figured for *Roccus sacatilis* by Merriman (1940) and *Archoplites interruptus* by Dineen and Stokely (1956), and exists in the representatives of Serranidae, Centrarchidae, Sciaenidae, Cichlidae, and Cirrhitidae that I stained or X-rayed. This condition is also figured by Hollister (1937b) for some iniomous fishes, and is shown in preparations of one beryciform fish (*Myripristis berndti*). Hollister (1936 and following) demonstrates that the number of hypurals may go at least as high as eight in some teleosts (Elopidae) or be reduced to three or two, presumably by fusion (in some Carangidae and Cyprinodontidae).

The scorpaenid, hexagrammid, zaniolepidid, and cottid representatives show a more derived condition; all have fewer than six free hypural elements in the caudal skeleton, presumably because of fusion. The four families illustrate three distinct stages in the fusion of caudal elements. The typical scorpaenid arrangement is that of hypurals 1 and 6 being free, while 2 and 3, and 4 and 5 are fused into lower and upper plates, respectively. This arrangement is illustrated for *Sebastes* and *Helicolenus* by Andriashev (1954). In *Pleurogrammus* and all species of *Hexagrammos* the upper and lower sets of primitively free hypurals are fused into upper and lower plates, each of which is suturally attached to the urostyle. *Oryzias* and *Ophiodon* have individual variations: hypural 6 is free in

Oxygobius and hypurals 1 and 2 appear weakly joined or sutured in *Ophiodon*.

Representatives of the Zaniolepididae and Cottidae are similar and have much more fusion than the Hexagrammidae. Each of the upper and lower sets of three hypurals is fused into a single plate and the upper plate also seems fused to the urostyle. This condition exists for all cottids (8 genera) examined and also is depicted for the cottids and comephorids of Lake Baikal by Taliev (1955).

The status of *Erilepis zonifer* and *Anoplopoma fimbria* (Anoplopomatidae) is uncertain. In *E. zonifer*, only juvenile specimens (about 1½ feet long) were obtainable. These indicate that hypurals 2 and 3 only are fused. Boiled and X-ray preparations of *A. fimbria* are difficult to decipher because the bones have a spongy texture and sutures are indistinct. However, the available evidence from juvenile and young adult *A. fimbria* suggests that a coossification exists between hypurals 2-3 and also 5-6. If these observations are adequate, both species show a condition primitive to that of the hexagrammids, zaniolepidids, and cottids. Also, the scorpaenid condition is distinct from the anoplopomatid, suggesting that these families are on distinct evolutionary lines within the Cottoidae.

No convincing example was found in the Perciformes of revision to a more primitive hypural arrangement by one member of a group that has, as a whole, a highly derived caudal skeleton. No examples are given in the literature that was examined. In theory this could occur by paedomorphosis (as described by De Beer, 1951). The caudal skeleton of *Pleurogrammus monopterygius* was carefully examined because the species is paedomorphic in numerous respects; however, the caudal skeleton of this species is essentially the same as that of *Hexagrammos* spp.

APPENDICULAR SKELETON

PELVIC GIRDLE.

No important differences in structure or attachment of the pelvic girdle exist between the members of the Serranidae, Cirrhitidae, Scorpaenidae, Hexagrammidae, and Zaniolepididae that were examined. Five soft pelvic rays are present in the Hexagrammidae and Zaniolepididae in contrast to the Cottidae, in which the number is reduced in all but a few primitive genera.

PECTORAL GIRDLE.

Numerous characters of the pectoral girdle have long been utilized in the classification of mail-cheeked fishes. These include the character of the junction between scapula and coracoid, the breadth of these bones, the shape of the radials that support the pectoral rays, and the fusion or free-

dom of the upper, or first, radial. Gill (1889) uses some of these characters for a few mail-cheeked representatives and Regan (1913) extends the species coverage. These works are supplemented by the detailed observations of Rendahl (1934a) and the numerous figures of Japanese scorpaenoid representatives by Matsubara (1943).

Nearly all degrees of separation of coracoid and scapula exist among representatives of various percoid groups. At one extreme these elements are well developed and in broad contact; at the other they are reduced and widely separated by cartilage or an open area. Serranids generally have the bones in contact, whereas the elements are separated in the Cottidae examined and evidently in all Comephoridae of Lake Baikal according to the figures of Taliev (1955). Separation of coracoid and scapula is considerable in the Triglidae and reaches an advanced degree in some Cyclopteridae (for examples see Andriashev, 1954).

Representatives of the Cirrhitidae, Scorpaenidae, Platycephalidae, and Zaniolepididae share the serranid condition, in which the scapula and coracoid are broadly in contact. Some variation occurs within the Hexagrammidae and Anoplopomatidae. In *Ophiodon elongatus* the scapula and coracoid are in contact, whereas the two elements are separated by a narrow band of cartilage in *Orylebius*, *Hexagrammos*, and *Pleurogrammus*, a condition intermediate between that of the serranids and cottids. In the Anoplopomatidae, *Anoplopoma* has the scapula and coracoid in contact but *Erilepis* appears to have these elements somewhat separated by cartilage (the *Erilepis* specimen, however, was a juvenile approximately one and one-half feet in total length and may not have represented the adult condition).

Cottids also depart markedly from the serranid condition in regard to shape of the radial elements in the pectoral girdle. Serranid representatives have elongate radials interspersed by large foramina, but cottids have square, flat, platelike radials, with the intervening foramina reduced or absent. Again, the hexagrammids are intermediate, as are the zaniolepidids—both have broadened radials and rather large foramina. The anoplopomatid condition is similar to that of the serranids.

A condyle, presumably for articulation of the uppermost pectoral ray, is developed on the upper edge of the scapula adjacent to the first radial in representatives of the Serranidae, Cirrhitidae, Platycephalidae, and in the anoplopomatid *Erilepis*. This condyle is absent in the representatives of the Scorpaenidae, Hexagrammidae, Zaniolepididae, Cottidae, and in *Anoplopoma*.

The first radial element is not ankylosed to the scapula in representatives of the Hexagrammidae, Zaniolepididae, and Anoplopomatidae. In the scorpaenid fishes it may be either suturally attached or fused to the scapula,

depending upon the genus. Seven of the twenty-six Japanese genera listed by Matsubara (1943) have the first radial fused to the scapula. The representatives of the Cottidae except *Scorpaenichthys marmoratus* have the first radial free. Taranets (1941) errs seriously in stating that *Scorpaenichthys marmoratus* is exceptional among all mail-cheeked fishes in having the first radial ankylosed to the scapula. The statement would seem accurate if "Cottidae" were substituted for "all mail-cheeked fishes."

Representatives of all pereiform fishes examined had the uppermost pectoral ray simple, and Rendahl (1934a) finds this to be true for all mail-cheeked fishes he examined. However, considerable variation occurs between the pereiform groups in the number of remaining rays in the pectoral fin that are branched. Rendahl notes that *Hexagrammos octogrammus* and *H. otakii* are exceptional among the cottoid representatives in having all of the remaining rays branched. In general, I find Rendahl's conclusions to be correct: the uppermost one or two are the only simple pectoral rays in adult representatives of *Oxylebius*, *Ophiodon*, and *Hexagrammos*. The same is true also for both species in the Zaniolepididae and in the Anoplopomatidae. A similar low proportion of simple pectoral rays is also found in some serranids but this condition is rare or absent among the cirrhitids, and the scorpaenids are quite variable in this character (Jordan and Evermann, 1905).

A noteworthy exception to the normal hexagrammid condition of having simple pectoral rays restricted to the one or two uppermost in the fin is found in adults of the hexagrammid genus *Pleurogrammus*, where all pectoral rays are simple. This condition is found only in juveniles of other hexagrammids. Its persistence in adult *Pleurogrammus* is strong evidence for the probable paeodomorphic mode of evolution of this genus.

DISCUSSION

Consideration of the osteological characters discussed in the previous sections gives strong evidence that some parts of the classification of mail-cheeked fishes as given by Regan (1913) and Berg (1940) are in need of rearrangement. The past classification, which is primarily the work of Regan, widely separates the superfamily Hexagrammoidae from the Cottoidae (two superfamilies are inserted between). Also, the families Hexagrammidae and Anoplopomatidae are grouped under the same superfamily, the Hexagrammoidae.

The osteological evidence indicates that the hexagrammids and zaniolepidids are early offshoots from the cottid evolutionary line and should be included in the cottoid superfamily. Although representatives of the Icelidae, the family placed first under the Cottoidae by Berg, were not examined, the hexagrammids should probably occupy the first position be-

cause their characters seem the most generalized among the living representatives of the cottoid superfamily. Second place should probably be occupied by the Zaniolepididae because the affinities between this family and the cottids are much stronger. The hexagrammid-cottid relationship is anticipated by Jordan and Evermann (1898), and Jordan (1905) notes that some of the more primitive cottids resemble hexagrammids quite closely and that the hexagrammids probably are primitive to both the cottids and *Zaniolepis*.

The Anoplopomatidae, in contrast, have few if any important affinities to the other mail-checked fish groups. The suborbital stay appears to be the sole character uniting at least three seemingly distinct evolutionary lines within the suborder—anoplopomatoid, scorpaenoid, and cottoid. It might be speculated that the suborbital stay originated independently in at least two of the groups and that the Cottoidei are a polyphyletic assemblage.

Head skeletons of the Hexagrammidae, Zaniolepididae, and Cottidae are very similar. Nearly all representatives have well-defined supratemporal canals that traverse the parietal elements, and all have a parasphenoid-pterosphenoid junction. These characters are also present in combination in some members of the Platycephalidae and Anoplopomatidae, which are not classed in the superfamily Cottoideae. However, in these forms the supratemporal canals are not well-defined structures but are submerged in the fissures of the posterior parietals; the canals are more difficult to distinguish, and bear a closer resemblance to those of the Scorpaenidae. Presence or absence of the parasphenoid-pterosphenoid junction should be used with caution in judging the affinities of percoid groups; this contact appears to have been independently evolved in some genera of Serranidae, and the elements are nearly in contact in examples of *Cirrhitus rivulatus* and one species of *Scorpaena*.

The head skeletons of hexagrammids and zaniolepidids are intermediate between the generalized condition of the scorpaenids and the more derived condition of the cottids in several additional respects. The presence of a basisphenoid definitely separates the Hexagrammidae and Zaniolepididae from the cottids and its absence in the cottids may be associated with reduced ossification of the myodome roof. The basisphenoid and myodome roof are delicate in the hexagrammids and zaniolepidids but otherwise as in the Scorpaenidae. In these respects the hexagrammids and zaniolepidids probably represent the ancestral condition of the cottids.

A similar relationship exists in regard to fusion and size of the upper pharyngeals. The most primitive condition is shown by representatives of the Scorpaenidae, Anoplopomatidae, and Platycephalidae, in which all three pairs of upper pharyngeals are approximately the same size. The third pair of pharyngeals is small in the hexagrammids and zaniolepidids

(usually one-half or less the size of the first pair), and the third pair lies close to the posterolateral edge of the much larger second pair. In contrast, the last two pairs are fused in the cottid representatives, and the resulting combined structure is similar in shape and in relative size to the last two closely associated pharyngeal pairs of the hexagrammids and zaniolepidids. The cottid condition, once again, could easily be derived from that of the hexagrammids and zaniolepidids.

Examples from the hexagrammid-cottid and the scorpaenoid lines are quite distinct in regard to condition and completeness of the suborbital series of bones; they are also quite distinct in regard to the degree of proximity shown by the exoccipital elements on the floor of the foramen magnum. All hexagrammid representatives and many of the cottids have a complete bony ring composed of five suborbital elements. The last element, the dermosphenotic, is loosely attached to the sphenotic. In the zaniolepidids the second and third elements appear fused. Other mail-cheeked fishes usually have several of the posterior suborbital elements missing, and also have the dermosphenotic firmly attached to the sphenotic. The exoccipital elements on the floor of the foramen magnum are widely separated in both hexagrammid and cottid representatives (except *Oryzias*), which contrasts strongly with the scorpaenid representatives, in which the exoccipitals are in broad contact. *Oryzias* is intermediate, having these elements in contact anteriorly and broadly separated posteriorly.

Anatomical and numerical relationships between vertebral column, spinous dorsal rays, and pterygiophores below the spinous dorsal fin are similar in the hexagrammids, zaniolepidids, and cottids. These fishes differ significantly from representatives of the superfamilies Scorpaenoidae and Platycephaloidae. In hexagrammids and cottids, the pterygiophores are nearly always single in the spaces between the neural spines beneath the spinous dorsal fin. Representatives of the Scorpaenidae, Triglidae, and Platycephalidae differ from the hexagrammid-cottid group in having pterygiophores doubled in at least one space in this region, a condition also found in the greater part of the spiny-rayed fishes that are not mail-cheeked. Both anoplopomatid species have some doubling of pterygiophores in their spaces, and therefore differ significantly from the hexagrammids, zaniolepidids, and cottids in this respect.

In rib relationships, the hexagrammids, zaniolepidids, and anoplopomatids differ from the other acanthopterygian representatives in having pleural and epipleural ribs inserted together on the parapophyses. The scorpaenids show what appears to be the more generalized condition, where the epipleural ribs are inserted on the pleurals. Cottids lack pleural ribs in an extensive anterior section of the vertebral column but possess "epi-

pleural" ribs that are attached to the vertebrae in this region. The cottid condition seems much more easily derivable from that of the hexagrammids, zaniolepidids, and anoplopomatids, in which the two types of ribs originate on vertebrae, than from that of the scorpaenids.

The caudal skeleton was found to be quite distinctive in many of the fish groups. The anoplopomatids show a presumably more primitive condition than do the scorpaenids, which have all but the first and last (1 and 6) hypurals coossified into a single dorsal and a single ventral plate. Hexagrammids have one or both of the bordering hypurals (1 and 6), which are free in the scorpaenids, ankylosed to their neighbors. In the zaniolepidids and cottids the hypural elements are fused into dorsal and ventral plates—and fusion reaches an extreme with fusion of the plates to each other and also to the urostyle.

In regard to the structure of the pectoral girdle, the hexagrammids are nearly intermediate between the scorpaenids and cottids. The coracoid and scapula are in contact in *Ophiodon* as in the zaniolepidid, scorpaenid, and platycephalid representatives. In the other hexagrammids the two elements are separated by cartilage, a condition shown in a much more extreme degree by the cottids. The radials of the hexagrammids and zaniolepidids are intermediate between the "anvil-shape" of most scorpaenids and the flat plates of the cottids. The pectoral girdle of *Anoplopoma* and *Erilepis* is quite similar to that of the scorpaenids. In regard to branched pectoral rays, the hexagrammids (except *Pleurogrammus*), zaniolepidids, and anoplopomatids, seem unique among the mail-cheeked fishes in having all but the uppermost one or two pectoral rays branched. In *Pleurogrammus*, a genus with a number of other larval characteristics, simple rays are retained.

SYNOPSIS

The summary given below of the preceding osteological discussion follows the classification of Berg (1940, 1955), which, for the mail-cheeked fishes, is but a slight modification of Regan's (1913) classification. (In some instances, characteristics are included that are not osteological but do appear to be outstanding morphological or biological features of a group. This follows the precedent of Regan (1913) and Berg (1940).) The characterizations are based upon Regan's key and synopsis, and my additions bear an asterisk. Additions not original with the present research bear an author citation. Recommended taxonomic changes above the family level (see preceding section) are not included because many of the mail-cheeked groups, particularly the anoplopomatids, cottids, and cottid allies, are in need of intensive study.

Superfamily SCORPAENOIDAE

Characters in common with the Hexagrammidae:

- Opisthotic extends forward to prootic (except *Ophiodon*).
- Basisphenoid usually present.
- Myodome roof osseous.
- Hypopalatine bones present and normally developed.

Characters absent in the Hexagrammidae:

- No parasphenoid-pterosphenoid contact.

1. **Scorpaenidae**

Characters in common with the Hexagrammidae:

- Head:* Posttemporal forked.
Three pairs of dentigerous upper pharyngeals.
Gill membranes free from isthmus (except *Ophiodon*).
- Axial:* Ribs present on all precaudal vertebrae.
Hypurals 2-3 and 4-5 fused.*
- Pectoral:* Radials anvil-shaped.
- Pelvic:* Fins usually I, 5 and normally developed.

Characters absent in the Hexagrammidae:

- Head:* Dermosphenotic fused to sphenotic.*
Third pair of upper pharyngeals as large or nearly as large as second pair.*
Seven branchiostegals.*
Usually no slit behind last gill arch (Jordan and Evermann, 1905).*
- Axial:* Pterygiophores usually paired in one or more spaces below spinous dorsal fin.*
Usually fewer than 37 vertebrae.
Hypurals 1 and 6 free.*
- Pectoral:* Coracoid and scapula in contact (except *Ophiodon*).

2. **Triglidae**

Characters in common with the Hexagrammidae:

- Head:* Posttemporal forked.
Three pairs of dentigerous upper pharyngeals.
Gill membranes free (except *Ophiodon*).
- Axial:* Ribs present on all precaudal vertebrae.
Hypurals 4 and 5 fused.*
- Pectoral:* Coracoid and scapula not in contact (except *Ophiodon*).
- Pelvic:* Fins I, 5 and normally developed.

Superfamily SCORPAENOIDAE — Cont.

2. **Triglidae** — Cont.

Characters absent in the Hexagrammidae:

- Head:* Second suborbital attached to lateral ethmoids.
Dermosphenotic fused to sphenotic.*
Upper limb of posttemporal developed into a triangular plate.
Armored.
- Axial:* Pterygiophores doubled in some spaces below spinous dorsal fin.*
Fewer than 37 vertebrae.
Hypurals 2 and 3 free.*
- Pectoral:* Radials platelike.
Lower rays free, simple, and specialized.

3. **Caracanthidae**

Characters in common with the Hexagrammidae:

- Head:* Posttemporal forked.
Three pairs of dentigerous upper pharyngeals.
- Pectoral:* Radials anvil-shaped.

Characters absent in the Hexagrammidae:

- Head:* Gill openings restricted to above pectorals.
- Axial:* Pleural ribs absent.
Vertebrae fewer than 37.
- Pectoral:* Coracoid and scapula in contact (except *Ophiodon*).

4. **Aploactidae**

Characters in common with the Hexagrammidae:

- Head:* Posttemporal forked.
- Anal fin:* Spines flexible.

Characters absent in the Hexagrammidae:

- Head:* Single pair of dentigerous upper pharyngeals.
- Axial:* Pleural ribs absent.
Vertebrae fewer than 37.
- Pelvic:* Fins 1, 2.
- Other:* Dorsal fin commencing on head.
Body scaleless.

5. **Synancejidae**

Characters in common with the Hexagrammidae:

- Head:* Posttemporal forked.

Superfamily SCORPAENOIDAE — Cont.

5. **Synancejidae** — Cont.

Pectoral: Some cartilage between scapula and coracoid.

Anal fin: Spines flexible.

Characters absent in the Hexagrammidae:

Head: Single pair of dentigerous upper pharyngeals.
Gill membranes attached to isthmus (except *Ophiodon*).

Axial: Pleural ribs absent.
Vertebrae fewer than 37.

Pectoral: First radial fused to scapula.

Pelvic: Fins of some species I, 4.
Innermost ray adnate to abdomen.

Other: Dorsal fin commencing on head.
Body scaleless.

6. **Pataecidae**

Characters in common with the Hexagrammidae:

Head: Posttemporal forked.
Gill membranes free from isthmus.

Characters absent in the Hexagrammidae:

Head: Suborbitals thin or sometimes membranous.
Epiotics united by a suture behind the supraoccipital.
Single pair of dentigerous upper pharyngeals.

Axial: Vertebrae fewer than 37.

Pelvic: Fins absent in some species.

Superfamily HEXAGRAMMOIDAE

1. **Hexagrammidae** (*Oryzias*, *Ophiodon*, *Hexagrammos* (including *Agrammus*), *Pleurogrammus*).

Distinctive characters:

Head: Opisthotic large, reaching prootic (except *Ophiodon*).
Five suborbitals and lachrymal present.*
Dermosphenotic loosely attached to sphenotic.*
Parasphenoid-pterosphenoid contact.
Myodome with osseous roof.
Basisphenoid present.
Supratemporal canals usually conspicuous.*
Posttemporal forked.
Three pairs of dentigerous upper pharyngeals.

Superfamily HEXAGRAMMOIDAE — Cont.

1. **Hexagrammidae** — Cont.

Third pair of upper pharyngeals small, one-half or less the size of the first pair in most species.*

Six branchiostegals.*

Gill membranes free from isthmus and broadly joined (except *Ophiodon*).

Large slit present behind the last gill arch.*

Adults usually with posterior nostrils reduced.*

Axial: Vertebrae 37–64.*

Dorsal fin spines begin on first pterygiophore or are doubled on the second.*

Pterygiophore series begins in first space behind cranium.*

Pterygiophores usually single in their spaces below spinous dorsal fin.*

Dorsal pterygiophores occupy approximately 81 per cent of the spaces available.*

Epipleural ribs present.

Pleural ribs present.

Pleural and epipleural ribs inserted together on parapophyses.

Hypurals 1, 2, 3 and 4, 5, 6 usually fused into plates (except *Oxylebius* and *Ophiodon*).*

Hypural plates not fused to urostyle.*

Pectoral: Coracoid and scapula not in contact (except *Ophiodon*).

Four anvil-shaped radials.

No pectoral condyle on scapula.*

All pectoral rays but uppermost one or two branched (except *Pleurogrammus*).*

Pelvic: Fins 1, 5 and normally developed.

Anal fin: Spines variable in number, 0–III, and flexible.*

2. **Anoplopomatidae** (*Anoplopoma*, *Erilepis*)

Characters in common with the Hexagrammidae:

Head: Basisphenoid present.*

Posttemporal forked.

Three pairs of dentigerous upper pharyngeals.

Six branchiostegals.*

Large slit behind last gill arch.*

Axial: Pleural ribs present.

Epipleural ribs present.

Superfamily HEXAGRAMMOIDAE — Cont.

2. **Anoplopomatidae** — Cont.

Pleural and epipleural ribs inserted together on parapophyses.

Pectoral: Four anvil-shaped radials.

All pectoral rays but uppermost one branched (except *Pleurogrammus*).*

Pelvic: Fins I, 5 and normally developed.

Characters absent in the Hexagrammidae:

Head: Opisthotic small, not contacting prootic (except *Ophiodon*).

Supratemporal canals inconspicuous.*

Third pair of pharyngeals nearly as large as second pair.*

Gill membranes attached to isthmus (except *Ophiodon*).

Branchiostegal membrane scaled.*

Axial: Doubled pterygiophores in some spaces below spinous dorsal fin.*

No pterygiophores in spaces 1-4.*

Hypurals 1, 2, and 4, 5, free.*

Pectoral: Coracoid and scapula in contact (except *Ophiodon*).

3. **Zaniolepididae*** (*Zaniolepis*, incl. *Xantocles*)

Characters in common with the Hexagrammidae:

Head: Opisthotic large and reaches prootic (except *Ophiodon*).

Posttemporal forked.

Parasphenoid-pterosphenoid contact.

Basisphenoid present.

Myodome with osseous roof.

Supratemporal canals conspicuous.*

Three pairs of dentigerous upper pharyngeals.

Third pair of upper pharyngeals less than one-half the size of the first pair.*

Six branchiostegals.*

A large slit behind the last gill arch.*

Axial: Pterygiophores single in their spaces below spinous dorsal fin.*

Pleural ribs present.

Epipleural ribs present.

Pleural and epipleural ribs inserted together on the parapophyses.

Superfamily HEXAGRAMMOIDAE — Cont.

3. **Zaniolepididae** — Cont.

Hypurals 1, 2, 3 and 4, 5, 6 fused into two plates (except *Oxylebius* and *Ophiodon*).*

Pectoral: No condyle on scapula.*

Four anvil-shaped radials.

All pectoral rays but uppermost one branched (except *Pleurogrammus*).*

Pelvic: Fins I, 5 and normally developed.

Characters absent in the Hexagrammidae:

Head: Four suborbitals (in addition to the lachrymal).*

Dermosphenotic firmly attached to the sphenotic.*

Axial: Dorsal fin spines begin posterior to first interneural space.*

Dorsal fin spines always single above the second interneural space.*

Dorsal and ventral hypural plates (formed from the fused hypurals) fused to each other and the urostyle.

Pectoral: Coracoid and scapula in contact (except *Ophiodon*).

Other: Scales "comb-shaped."*

Lateral line scales without perforations.*

Superfamily PLATYCEPHALOIDAE

1. **Platycephalidae**

Characters in common with the Hexagrammidae:

Head: Hyopalatine bones normally developed.

Parasphenoid-pterosphenoid contact.

Basisphenoid present.*

Opisthotic large and extending to prootic.

Posttemporal forked.

Three pairs of dentigerous upper pharyngeals.*

Pectoral: Four radials.

Pelvic: Fins I, 5.

Characters absent in the Hexagrammidae:

Head: Parasphenoid-frontal contact.

Third pair of upper dentigerous pharyngeals larger than the first pair.*

Seven branchiostegals.*

Skull flattened.

Superfamily PLATYCEPHALOIDAE — Cont.

1. **Platycephalidae** — Cont.

Axial: Pleural ribs attached to the epipleurals.
Epipleural ribs sessile.
Vertebrae fewer than 37.
First and sixth hypurals free.*

Pectoral: Coracoid and scapula contact (except *Ophiodon*).
Condyle on scapula.*
Radials short square plates.
Simple rays present in addition to uppermost one.*

Pelvic: A large oval space enclosed by the girdles (Matsubara and Ochiai, 1955).*

Anal fin: Spines absent (Matsubara and Ochiai, 1955).*

Superfamily HOPLICHTHYOIDAE

1. **Hoplichthyidae**

Characters in common with the Hexagrammidae:

Head: Basisphenoid present.
Opisthotic large and extending to prootic (except *Ophiodon*).
Posttemporal forked.

Axial: Epipleurals inserted on parapophyses.

Pectoral: Four anvil-shaped radials.

Characters absent in the Hexagrammidae:

Head: Myodome roof not osseous.
Palatine and pterygoid form a long slender rod.
No mesopterygoid; metapterygoid reduced.
Interopercle absent (Matsubara and Ochiai, 1955).*

Axial: Pleural ribs absent.
Vertebrae fewer than 37.

Pectoral: Coracoid and scapula contact (except *Ophiodon*).
Interradial foramina closed by an osseous membrane.
Some pectoral rays detached (Matsubara and Ochiai, 1955).*

Anal fin: Spines absent (Matsubara and Ochiai, 1955).*

Other: Scales restricted to lateral line (Matsubara and Ochiai, 1955).*

Superfamily CONGIOPODOIDAE

1. **Congiopodidae**

Characters in common with the Hexagrammidae:

Head: Opisthotic large, contacting or nearly contacting the prootic.

Three pairs of dentigerous upper pharyngeals.

A single nostril on each side.

Axial: Pleural ribs present.

Vertebrae 39.

Pectoral: Radials anvil-shaped.

Characters absent in the Hexagrammidae:

Head: Posttemporal simple.

Posttemporal forms an integral part of the skull.

Gill openings restricted to a region above the pectorals.

Dorsal fin: Originates on the head.

Pectoral: Coracoid and scapula contact (except *Ophiodon*).

Superfamily COTTOIDAE

Characters in common with Hexagrammidae:

Posttemporal forked.

Epipleural ribs present.

Precaudal vertebrae with epipleurals sessile or on short parapophyses.

Characters absent in the Hexagrammidae:

No basisphenoid.

Dentigerous upper pharyngeals restricted to one or two pairs.

Pleural ribs absent or developed on a few posterior precaudals only.

Pectoral interradi al foramina small or absent.

1. **Icelidae*** (*Icelus*, *Ereunias*, *Marukawichthys*), Berg (1940)

Characters absent in the Hexagrammidae:

Head: Vomer and mesethmoid unossified.

Opisthotic large, forming the upper margin of the foramen magnum.

Vagus foramen in opisthotic.

2. **Cottidae**

Characters in common with the Hexagrammidae:

Head: Parasphenoid-pterosphenoid contact.

Superfamily COTTOIDAE — Cont.

2. **Cottidae** — Cont.

Dermosphenotic loosely attached to the sphenotic.*

Six branchiostegals in most species.*

Gill membranes connected (except *Ophiodon*) (Jordan, 1929).*

Axial: Pterygiophores single in their spaces beneath the spinous dorsal fin.*

Pterygiophores begin with the first dorsal space.*

Dorsal fin: Spines begin with the first pterygiophore.*

Characters absent in the Hexagrammidae:

Head: Opisthotic small, not contacting prootic (except *Ophiodon*).

Axial: Hypurals fused into plates that are fused to the urostyle.*

Dorsal fin: Spinous and soft sections usually separate.

Pectoral: Coracoid and scapula widely separated.

Radials platelike.

Interradial foramina absent.

Simple rays in lower half of fin.*

Pelvic: Fins I, 4 or fewer in many species (Jordan, 1905).*
(Fins absent in *Ascelichthys*.)

Anal fin: Spines absent.

3. **Cottocomephoridae*** (regarded as a subfamily of Cottidae by Taliev, 1955).

Characters very similar to those of the Cottidae. Limited in its distribution to Lake Baikal, U.S.S.R.

4. **Comephoridae**

Characters in common with the Hexagrammidae:

Axial: Vertebrae 48–50.

Characters absent in the Hexagrammidae:

Head: Suborbital stay rudimentary.

Axial: Pleural ribs absent.

Pectoral: Posteleithra absent.

Pelvic: Fins absent.*

Other: Viviparous, limited to Lake Baikal, U.S.S.R.*

Superfamily COTTOIDAE — Cont.

5. **Normanichthyidae**.^{*} For osteology see Clark (1937), Norman (1938), and Tortonese (1939).

Characters in common with the Hexagrammidae:

Head: Unarmed.

Pelvic: Fins I, 5.

Other: Body covered with etenoid scales.

Characters absent in the Hexagrammidae:

Axial: No pleural ribs.

Hypurals 4, 5, 6 separate (Tortonese, 1939).^{*}

6. **Cottunculidae**

Characters absent in the Hexagrammidae:

Head: Opisthotic small (except *Ophiodon*).

No parasphenoid-pterosphenoid contact.

Pelvic: Incomplete (Jordan, 1905).^{*}

Other: Scales absent (Jordan, 1905).^{*}

7. **Psychrolutidae**

Characters in common with the Hexagrammidae:

Axial: Vertebrae 40.

Characters absent in the Hexagrammidae:

Head: Parasphenoid forms a complete interorbital septum.

Branchiostegals seven (Taranets, 1941).^{*}

Flattened.

Pectoral: Coracoid and scapula widely separated.

8. **Agonidae**

Characters in common with the Hexagrammidae:

Head: Parasphenoid-pterosphenoid contact.

Characters absent in the Hexagrammidae:

Head: Suborbitals completely fill the cheek.

Myodome roof reduced.

Pectoral: Coracoid and scapula widely separated by cartilage.

Other: Body completely or almost completely invested in bony plates.

9. **Cyclopteridae**

Characters in common with the Hexagrammidae:

Axial: Vertebrae 29–44, the range partially overlapping that of the Hexagrammidae.^{*}

Superfamily COTTOIDAE — Cont.

Characters absent in the Hexagrammidae:

Head: Olfactory nerve not entering orbit.*

Pterosphenoids absent.

Pectoral: Coracoid and scapula widely separated by cartilage.

Pelvic: Fins form a sucking disc.

Other: Spinous dorsal fin separate or absent.

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